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Surface burning in a mature stand of *Pinus resinosa* and *Pinus strobus* in Michigan: effects on understory vegetation

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Abstract. Beginning in 1991, periodic surface fires (frontal fire intensities <200 kW m^{-1}) were introduced into a mixed red pine (*Pinus resinosa* Ait.) and white pine (*P. strobus* L.) plantation (dbh 16–60 cm). Replicated plots of 0.4–0.5 ha were either burned three times at biennial intervals (early May of 1991, 1993, and 1995), burned once (early May 1991), or not burned. Measurements were conducted during the 1994 and 1995 growing seasons. The pine overstory was largely unaffected by the fires. The understory on unburned plots contained 16 111 large seedlings (>1 m, ≤ 1.9 cm dbh) and 3944 saplings (2.0–5.9 cm dbh) per ha, consisting of 23 woody angiosperm taxa. Plots burned once contained 60% of the large seedlings, 7% of the saplings, and 6 fewer taxa than unburned plots. No large seedlings and few saplings were found in plots burned biennially. Cover of low (<1 m) woody and herbaceous vegetation in plots burned once or three times was twice that of unburned plots, even in the growing season immediately following the May 1995 re-burn. Recovery of low vegetative cover in the re-burned plots was rapid, exceeding that in once-burned or unburned plots by late summer following the burn. Species richness of low vegetation was 20–25% higher in burned than unburned plots, except in the year immediately following reburning. Taxa dominating this site following burning were *Sassafras albidum* (Nutt.) Nees, *Rubus* spp., *Phytolacca americana* L., and *Dryopteris spinulosa* (O.F. Müll.) Watt. Restoration of low-intensity surface fires to ecosystems dominated by mature red pine or white pine is feasible, but major changes in understory structure and composition will occur.

Keywords: prescribed fire, fire frequency, restoration, diversity, natural regeneration, *Pinus resinosa*, *Pinus strobus*, *Sassafras albidum*, *Rubus* spp., *Phytolacca americana*, *Dryopteris spinulosa*

Introduction

Fire has been a pre-eminent natural process shaping many forest ecosystems in the Great Lakes Region of North America. Before European settlement, periodic fires of varying intensity swept through pine forests in this region at intervals of 5–50 years (Maissurow 1941; Van Wagner 1970; Burgess and Methven 1977; Pyne 1982; Rouse 1988; Bergeron and Brisson 1990; Engstrom and Mann 1991; Guyette *et al.* 1995). Fire scars can still be seen on the boles of trees in the few remnant old growth pine forests, attesting to their visitation by periodic fire. However, since the implementation of coordinated fire prevention and suppression activities by wildland management agencies beginning in the 1920s, the pine-fire cycle has largely been broken.

Red pine (*Pinus resinosa* Ait.) and white pine (*Pinus strobus* L.), two commercially important pine species common to the Great Lakes Region, can tolerate low-intensity surface fires in the understory, provided their crowns are high enough above the ground to escape scorching damage (Olson and Weyrick 1987; Dickmann 1993; McRae *et al.* 1994). In addition, the insulating quality of pine bark is excellent, minimizing cambial damage (Reifsnyder *et al.* 1967). The bark's heat resistant quality is augmented by vigorous resin flow that seals off moderate cambial wounds caused by fire (Heinselman 1981), although this resin is highly flammable and may cause the wound to enlarge following another fire, producing a catface. Underburning usually does not adversely affect overstory tree growth, provided that crown scorch is limited to <50% of the crown (Van Wagner 1970; Methven and Murray 1974; Alban 1977; McRae *et al.* 1994). In fact, Lunt (1950) observed that 20 years of annual underburning actually increased height and volume growth in red pine stands in Ontario.

Restoration of surface fires in ecosystems where mature pines dominate is a viable management option, especially where pressure to manage from an ecosystem perspective is strong (Arno 1996). Besides ecosystem restoration, other

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benefits from underburning (Olson and Weyrick 1987; Wade and Lunsford 1989; Dickmann 1993; McRae *et al.* 1994) include control of understory woody plants; improved habitat for wildlife, especially if combined with thinning (Rogers *et al.* 1996; Bender *et al.* 1997); control of insects and diseases; thinning overstocked stands; stimulation of pine regeneration; recycling of nutrients tied up in litter; reduction of wildfire hazard; and more pleasing aesthetics. For these reasons, fire needs to be part of the silvicultural repertoire of managers of pinelands in the Great Lakes Region and elsewhere.

Before prescribed burning is widely applied, the effects of fire on all components of red pine and white pine ecosystems need to be better understood. Few data are currently available upon which to build this understanding. Our previous studies have begun to describe the effects of periodic low-intensity prescribed surface fires on red pine stands in northern Michigan (Dickmann *et al.* 1987; Dickmann 1993; Henning and Dickmann 1996). The study reported here was initiated to define the ecological responses of a mature, mixed pine plantation in southern Michigan to the introduction of periodic fire. The major objectives of this study were to quantify effects of periodic burning on (1) responses of the vegetation and (2) activity and diversity of carabid beetles (Neumann 1997). This paper reports the effects of fire on vegetation.

Methods

Experimental site and design

The study was conducted at The W.K. Kellogg Experimental Forest, located in Kalamazoo County in the south-western lower peninsula of Michigan, USA (latitude 42^{o} 22′ N, longitude 85^{o} 20′ W). This experiment was established within Compartment 7 of the forest, a 4-ha mixed plantation of red pine and white pine. The stand was established in 1932 on an eroding hillside, which slopes from east to west, with a 1 ha flat area on the western-most side. The stand has been variably thinned several times since the 1950s. Soils consist of well-drained sandy loams of the Kalamazoo and Oshtemo series, derived from glacial till and outwash parent material. The Oshtemo soils are classified as coarse-loamy, mixed, mesic Typic Hapludalfs; Kalamazoo soils are fine-loamy, mixed, mesic Typic Hapludalfs. Site index is 21 m at 50 years on the upper slope positions and approximately 2 m higher on the lower flat; site index also is slightly higher on the Kalamazoo soil.

Burning

The study was established in 1991 to examine the ecological responses to low-intensity surface fires ignited at different intervals. The plantation was divided into nine plots 0.4–0.5 ha in size and one of three treatments assigned to each: unburned (control); burned biennially; and burned every 6 years. Treatment plots were arranged in a randomized complete block design with three replications. Replicates were assigned to blocks based on slope position (upper, middle, lower flat). Plots in the biennial-burn treatment had been burned twice with low intensity surface fires (May 1991 and May 1993) when the measurements reported here were initiated in 1994 and then were re-burned in May of 1995. Six-year-burn plots had been burned only once, in May 1991.

The prescription for the burns in this fueltype—C5: Red and White Pine (Canadian Forest Service 1999)—called for strip headfires with drip-torch ignitions. Successive strips were approximately 8 m apart on the flatter areas and somewhat closer on the steepest slopes to keep fire intensities within prescription. The critical parameter in our prescription for fire behavior was flame length or frontal fire intensity (Alexander 1982); our objective was to lose as few overstory trees to fire as possible. Based on our experience and others (Van Wagner 1973; Reinhardt and Ryan 1988; McRae *et al.* 1994), average flame lengths <0.5 m (frontal fire intensity <58 kW m^{-1}) and maximum flame lengths of 1 m (260 kW m^{-1}) will minimally scorch the crowns of mature red pine and white pine, yet provide adequate understory top kill.

Fireline weather conditions under the pine canopy were measured immediately before the first ignitions on a particular day (1000 to 1200 solar time) and then at least hourly thereafter until the fires were out (1400 to 1500 solar time). Temperature and relative humidity were measured with an electronic thermo-hygro probe (Solomat Instrumentation Division, Stamford, CT, USA) and wind speed was estimated with a mechanical wind meter. Flames lengths were estimated visually. Rates of spread were determined by timing the rate of burnout between successive ignition strips throughout the study site. Fuel moisture was not measured directly; if red pine needles on the soil surface snapped cleanly when bent, fine fuel moisture was judged to be within prescription boundaries.

As an aid to interpreting fire behavior, components of the Canadian Forest Fire Weather Index System—fine fuel moisture code, duff moisture code, drought code, initial spread index, buildup index, and fire weather index—were calculated (Canadian Forest Service 1987; Stocks *et al.* 1989). Daily weather data from the third day following the final melting of the winter snow or 15 March, whichever came later, to the day of each fire were used in these calculations. These data came from an automated weather station at the Kellogg Biological Station, 6.4 km from the study site.

Vegetation sampling

The ground flora stratum of understory vegetation was sampled every 4 weeks throughout the 1994 and 1995 growing seasons (May through September) to characterize treatment differences. This stratum was divided into herbaceous plants and woody seedlings <1 m tall. Species richness, frequency, and relative ground cover in this stratum were sampled by first systematically locating six subplot centers on a 15 m grid in each treatment plot (54 total). All but three centers were >2 m from the main plot edge. A 1 m^2 subplot was located 2 m from each center point on random azimuths in 1994, with a different randomization for each sampling. Species coverage in each subplot was occularly estimated. During 1995, six fixed-location, 1 m^2 subplots per treatment plot were established within 2 m of each center point so that changes in cover of ground flora could be assessed over the growing season.

All other vegetative strata were sampled at the end of the 1995 growing season. Density of the woody understory >1-m tall was determined using a 10 m^2 subplot nested on each 1 m^2 subplot. These data were expressed as total number of stems per ha in two strata; large seedlings— >1 m tall, ≤1.9 cm diameter at breast height (dbh)—and saplings—2.0–5.9 cm dbh. This sampling protocol was designed to allow vegetative comparisons among treatments and (in 1995) among dates. Basal area and tree dbhs of the overstory stratum were determined using variable radius subplots established with a 10-basal area factor (English) angle gauge at each center point.

Statistical analysis

Statistical analysis used the SAS System computer software (Stokes *et al.* 1995). An α value of 0.05 was used to test treatment means for significant differences. Vegetation data were analysed using standard linear ANOVA techniques to test for differences among the three treatments, after first testing for normality and homogeneity of variance. Data for tree and understory sapling and seedling data were analysed as a randomized complete block design using the SAS generalized linear model procedure.

Comparison of ground flora data between years was not possible due to the different sampling procedures used. Ground flora data for 1994 were collected from subplots randomly located at each sampling date; thus comparisons among dates were not possible. These data were summarized as the year-long average percentage coverage of woody and herbaceous ground flora in each treatment. The 1995 ground flora data were collected from fixed-location subplots randomly located at the beginning of the sampling year to allow comparison among treatments by date. Ground flora data were summarized separately as the total percentage coverage of small woody seedlings and herbaceous vegetation classes per subplot for each sampling date for use in a split-plot ANOVA design (split for dates) and in regression analysis. Measures of total annual percentage coverage and absolute frequency were calculated by summing across replications within each burning treatment. Relative frequency was then calculated using the sum of absolute frequencies for all ground flora species in each treatment. Average total annual percentage coverage was calculated by dividing the total annual percentage coverage for each species by the number of subplots (n = 18) in each treatment.

Results and discussion

Fire behavior

Wind speed in the pine stand during the burns usually was <3.2 km h^{-1}, with occasional gusts ≥ 8 km h^{-1}, especially upslope near the south edge of the study area which bordered a clearing (Table 1). During the burns ambient temperature varied from 16 to 32°C and relative humidity from 20 to 40%, depending upon the particular day (Table 1).

All fires burned within prescription (<1 m flame lengths), with minimum scorching damage to the crowns of overstory trees. Fewer than 10 trees were severely scorched (>80% needle loss), principally by the 1993 fires. Most of them eventually died. This scorching occurred near the top of the ridge that runs across the site, where winds were gusty and the strip headfires ran uphill. Top-kill of the understory in the burned plots was nearly complete. However, a few unburned islands <20 m^2 were left within the plots after the 1991 and 1995 fires, primarily in the flat at the base of the slope where winds were usually very light and spring green-up was further advanced. Even in areas where fire intensities were greatest, no more than the top 1.5 cm of the needle-leaf litter layer was consumed (fuel-weight reduction was not measured), leaving the humus (O_2) layer beneath intact. Furthermore, no downed woody fuels on the forest floor >2.5 cm in diameter were consumed.

The Canadian Forest Fire Weather Index (FWI) components in Table 1 would predict low-vigor surface fires (Alexander and DeGroot 1988), which is what occurred on all three burning dates. FWI fuel moisture codes and behavior indices were highest for the 1993 fires, leading to greater frontal fire intensities on that date, although still within prescription. On the other hand, FWI components for the 1995 fire predicted somewhat marginal fire behavior (Van Wagner and Methven 1978), and the fires did not carry well, especially over the lower portions of the study site. Fire behavior also followed closely that predicted by U.S. Forest Service Fire Behavior Fuel Model 9 (Anderson 1982).

Fire behavior was variable across the study site on each date, primarily due to inconstant wind speed and direction, variable topography, apparent differences in fuel moisture,

Table 1. Fireline weather and fire weather index components for three prescribed burning dates

Fireline weather is the range of hourly measurements on-site, beneath the pine canopy, during each burn. All fires occurred during the daily period 1000 to 1500 solar time. Wind direction and speed fluctuated across the experimental site on each date primarily due to variably sloping topography. FFMC, fine fuel moisture code; DMC, duff moisture code; DC, drought code; ISI, initial spread index; BUI, buildup index; FWI, fire weather index. R.H., relative humidity

Date of fire	Fireline weather			Canadian Forest Fire Weather Index System					
	Temp. (°C)	R.H. (%)	Wind (km h^{-1})	FFMC	DMC	DC	ISI	BUI	FWI
10 May 1991	26–29	32–40	<3.2, gusts to 8	90.5	23	76	6.5	26	11.6
10 May 1993	28–32	20–22	<3.2, occasional gusts to 8	92.7	33	84	8.1	34	15.6
3 May 1995	16–22	23–27	<3.2, steady	89.0	18	90	4.5	24	8.1

Table 2. Overstory basal area means (± standard deviations) and the proportion of total basal area in each of the major species groups by treatment in 1995

Basal area means followed by the same letter are not significantly different (α = 0.05)

Burning treatment	Total basal area (m^2/ha)	*Pinus strobus* L. (%)	*Pinus resinosa* Ait. (%)	Misc. hardwoods (%)
Biennial burns	47.5 ± 11.2a	37	61	2
Burned once	46.7 ± 8.4a	32	64	4
Unburned	48.8 ± 7.9a	35	61	4

Table 3. Mean large woody seedling (>1 m, ≤ 1.9 cm dbh) and sapling (2.0–5.9 cm dbh) density per ha (± standard deviations) among burning treatments in 1995

Means in any column followed by the same letter are not significantly different ($\alpha = 0.05$). Estimates of saplings in biennially burned plots reflect data outliers—saplings growing at the edges of plots or in unburned patches

Burning treatment	Large seedlings	Saplings
Biennial burns	0.0 ± 0.0a	166 ± 1130a
Burned once	9 277 ± 7870b	277 ± 960a
Unburned	16 111 ± 9010c	3944 ± 1860b

and variation in understory composition, structure and green-up. The backfire and headfire fronts of each strip exhibited different behavior, due to their interaction with slope position. Flame lengths during each burn usually ranged between 0.2 m and 0.8 m (frontal fire intensities of 8–160 kW m^{-1}; Alexander 1982), with rare fire whirls (McPherson *et al.* 1990) on the upper slope to 2 m in height (1170 kW m^{-1}). Occasionally fire would climb 2–4 m up the boles of trees, especially red pines, using bark flakes as ladder fuel and briefly igniting dead branch stubs. Highest fire intensities on the study site consistently occurred on the mid-slope and upper slope positions (blocks 2 and 3). The prescription called for a fire to be extinguished or cooled down if flame lengths consistently exceeded 1 m, but this condition never occurred. On the lower flat (block 1) in areas of intense green-up, fires occasionally would not carry and re-ignitions were required. Rates of spread varied from >2.5 m min^{-1} for headfires on the steepest slopes, to <0.5 m min^{-1} for slow-moving backfires on the lower flat.

Overstory and woody understory

Species density and composition of the mixed pine overstory across the plantation were relatively homogeneous. Average red pine and white pine densities were 131 and 93 trees per ha, respectively. Red pine dbhs ranged from 16 to 40 cm and white pine dbhs from 20 to 60 cm, with the largest trees of both species found on the lower slope positions.

The three treatments also contained similar average basal areas of red pine and white pine, approximately 29 and 16 m^2 per ha, respectively (Table 2). A one-way analysis of variance for overstory basal area indicated no significant differences among treatments and blocks despite a history of variable thinning.

The effects of periodic burning were apparent in the ground flora, large seedling, and sapling strata. The understory of plots burned biennially was composed chiefly of low herbaceous and woody ground flora. Only three saplings (2.0–5.9 cm dbh) were observed in 18 sample subplots of 10 m^2; two observations occurred near the edges of treatment areas, and one sapling occurred in an area of the plot where the previous fire did not carry. These observations were considered outliers and excluded from further analysis. Plots burned biennially also were virtually devoid of large seedling-size woody vegetation (>1m tall; 0–1.9 cm dbh). Nevertheless, ANOVAs for sapling and large seedling data included all burn treatments.

Unburned plots were well stocked with sapling-size advanced regeneration, averaging 3944 stems per ha in the 2.0–5.9 cm dbh class. Saplings were scarce, however, in the once-burned plots, with fewer than 300 stems per ha (Table 3). Multiple comparison tests indicated that differences in sapling density were significant between burned and unburned treatments ($P = 0.0001$), but not between burn treatments. No differences among blocks were found.

Large-seedling density on the once-burned plots was roughly half the density of the unburned plots (Table 3), with 9277 and 16 111 seedlings per ha, respectively, but no large seedlings were observed on plots burned biennially. Significant differences in seedling density occurred among the treatments ($P = 0.0001$) but not among blocks. Multiple comparison procedures indicated significant differences among all three treatments.

These data resemble the results of prescribed burning studies in northern Lower Michigan red pine stands. Henning and Dickmann (1996) reported sapling densities of 210, 385, and 4336 stems per ha for biennial burn interval, 5-year burn interval, and unburned treatments, respectively. They also noted significant differences among these treatments for seedling density, following a pattern similar to ours. Niering *et al.* (1970) and Hodgkins (1958) reported that frequent low-intensity prescribed fires kill most stems <10 cm dbh, while larger trees escape relatively unscathed. Prescribed fire effects are short-lived in the absence of repeated burning, however; hardwood regrowth may reach heights of up to 1.8 m after only three growing seasons (Hodgkins 1958).

Effects of burning on woody species composition in our study were very evident in the large-seedling stratum (Table 4). Plots burned biennially contained no large seedlings. Plots burned only once contained about half as many stems per ha as those unburned and were dominated by common buckthorn (*Rhamnus cathartica*) and sassafras (*Sassafras albidum*). *Viburnum* spp. and tulip poplar (*Liriodendron tulipifera*) were found only on burned plots. Unburned plots contained greater densities of thin-barked species and shrubs, including black cherry (*Prunus serotina*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), bush honeysuckle (*Diervilla lonicera*) and *Carya* species. Several species occurred only on unburned plots: hackberry (*Celtis occidentalis*), flowering dogwood (*Cornus florida*), hornbeam (*Carpinus caroliniana*), black oak (*Quercus velutina*), honeysuckle, green ash (*Fraxinus

Table 4. Mean large woody seedling (>1 m, ≤1.9 cm dbh) density per ha by taxa in once-burned and unburned treatments in 1995

No large seedlings were observed in biennially burned plots

Taxa	Burning treatment	
	Burned once	Unburned
Acer negundo L.	56	56
Acer rubrum L.	833	3,611
Acer saccharum Marsh.	667	1,111
Carpinus caroliniana Walt.	0	56
Carya spp.	167	722
Celtis occidentalis L.	0	111
Cornus florida L.	0	56
Corylus cornuta Marsh.	111	167
Diervilla lonicera Mill.	0	1,278
Fraxinus americana L.	111	333
Fraxinus pennsylvanica Marsh.	0	333
Liriodendron tulipifera L.	222	0
Morus spp.	56	111
Prunus avium (L.) L.	56	167
Prunus serotina Ehrh.	500	3,167
Quercus alba L.	389	667
Quercus rubra L.	667	667
Quercus velutina Lam.	0	333
Rhamnus cathartica L.	1722	944
Rhamnus frangula L.	444	778
Sambucus spp.	444	444
Sassafras albidum (Nutt.) Nees	2389	556
Viburnum spp.	444	0
Vitis spp.	0	389
Zanthoxylum americanum Mill.	0	56

pennsylvanica), *Vitis* species, and prickly ash (*Zanthoxylum americanum*) (Table 4). Burning apparently did not result in increased establishment of large oak seedlings; unburned plots contained more white oak (*Q. alba*) and the same number of red oak (*Q. rubra*) than once-burned plots.

Sapling species composition in the once-burned and unburned plots also reflects the frequency of disturbance. Once-burned plots contained only 279 stems per ha of sassafras, hickory, red maple, and black cherry (Table 5), and lacked the very tolerant sugar maple, dogwood, and *Rhamnus* spp. Unburned plots, on the other hand, contained a rich sapling stratum—13 species and 3947 stems per ha—dominated by red maple, black cherry, green ash, white ash (*F. americana*), *Rhamnus* spp., and sassafras.

Ground flora

Burned plots contained a rich community of ground flora species (Tables 6–11), which was visually discernible from unburned areas of the stand where low vegetation was relatively depauperate. Plots burned biennially contained a thick undergrowth which generally averaged <1 m in height. Once-burned plots contained a greater composition of woody ground flora species than recently reburned plots in 1995, but appeared similar in 1994 to plots burned biennially, which were then in their second year of recovery. Ground flora in once-burned plots averaged 1 – 1.5 m in height.

Table 5. Mean sapling (2.0–5.9 cm dbh) density per ha by taxa in once-burned and unburned treatments in 1995

Saplings growing at the edges or in unburned patches in biennially burned plots have not been included. No other saplings were found in these plots

Taxa	Burning treatment	
	Burned once	Unburned
Acer rubrum	56	1778
Acer saccharum	0	167
Carya spp.	56	111
Cornus florida	0	56
Diervilla lonicera	0	56
Fraxinus americana	0	222
Fraxinus pennsylvanica	0	56
Populus spp.	0	56
Prunus serotina	56	833
Quercus rubra	0	56
Rhamnus cathartica	0	222
Rhamnus frangula	0	56
Sassafras albidum	111	278

Table 6. Mean percentage cover of small (<1 m) woody seedlings in 1994 by burning treatment

Only taxa with ≥0.1 percentage cover are shown, but totals include all species. Totals with same letter are not significantly different ($\alpha = 0.05$, d.f. = 249, $n = 90$)

Taxa	2 biennial burns	Burned once	Unburned
Acer spp	0.44	1.57	2.11
Carya spp.	0.38	0.51	0.28
Diervilla lonicera	0.40	0.40	0.64
Fraxinus spp.	0.24	0.28	0.23
Parthenocissus quinquefolia (L.) Planch.	11.11	11.98	4.88
Pinus spp.	0.32	0.23	0.73
Prunus spp.	0.27	0.36	1.10
Quercus spp.	0.87	1.89	0.50
Rhamnus cathartica	1.50	1.90	0.53
Rhamnus frangula	0.28	—	—
Rhus spp.	0.21	0.26	—
Rosa spp.	—	0.11	—
Rubus spp.	16.73	12.66	2.73
Sambucus spp.	0.48	0.01	0.08
Sassafras albidum	4.78	4.78	2.68
Smilax hispida Muhl.	0.89	0.24	0.87
Tilia americana L.	—	0.13	0.50
Toxicodendron radicans (L.) Kuntze	1.34	1.44	0.74
Vitis spp.	0.43	1.82	1.35
Total ± s.d.	40.7 ± 38.0	40.6 ± 33.5	20.0 ± 24.1
Student-Newman-Keuls	a	a	b
Tukey's HSD	a	a	b

Table 7. Mean percentage cover of herbaceous ground flora in 1994 by burning treatment

Only species with ≥0.1 percentage cover are shown, but totals include all species. Totals with same letter are not significantly different (α= 0.05, d.f. = 249, n = 90).

Taxa	2 biennial burns	Burned once	Unburned
Apios americana Medic.	1.09	1.62	0.29
Arctium minus Schk.	0.07	1.00	—
Asclepias syriaca	0.11	0.83	—
Aster spp.	0.14	0.91	0.08
Carex spp.	0.08	0.28	0.03
Circaea quadrisulcata (Maxim.) Franch. & Sav.	1.09	0.29	0.57
Desmodium glutinosum (Muhl.) Wood	0.40	0.18	—
Dryopteris spinulosa (O.F. Müll.) Watt	3.24	4.39	2.88
Fragaria virginiana Duch.	0.12	0.20	0.03
Gallium spp.	0.30	0.52	0.43
Hieracium aurantiacum L.	0.07	0.33	—
Lactuca scariola L.	0.14	0.07	—
Mitchella repens L.	—	0.33	—
Osmarhiza claytoni (Michx.) Clarke	0.06	0.33	0.18
Oxalis acetosella L.	0.22	0.06	—
Phryma leptostachya L.	0.16	0.32	0.23
Phytolacca americana L.	4.84	1.26	0.08
Pilea pumila (L.) Gray	0.40	0.02	0.29
Poa spp.	0.17	0.37	0.03
Podophyllum peltatum L.	0.01	0.20	—
Polygonatum biflorum (Walt.) Ell.	0.26	0.63	0.29
Rumex acetosella L.	0.13	0.10	—
Taraxacum officinale Weber	0.13	0.11	0.04
Trillium spp.	0.14	0.03	—
Viola spp.	2.69	0.67	1.74
Total ± s.d.	16.4 ± 22.4	15.4 ± 20.0	7.3 ± 12.4
Student-Newman-Keuls	a	a	b
Tukey's HSD	a	a	b

Table 8. Mean percentage cover of small (<1 m) woody seedlings in 1995 by burning treatment

Only species with ≥0.1 percentage cover are shown, but totals include all species. Totals with same letter are not significantly different (α= 0.05, d.f. = 270, n = 108)

Taxa	3 biennial burns	Burned once	Unburned
Acer spp.	0.15	1.53	2.40
Berberis thunbergii DC.	—	0.33	0.03
Carya spp.	—	0.69	0.03
Celastrus scandens L.	0.47	—	1.83
Diervilla lonicera	—	0.58	0.50
Parthenocissus quinquefolia	6.58	13.12	3.36
Pinus spp.	0.11	0.07	0.71
Prunus spp.	—	0.75	1.44
Quercus spp.	0.21	1.04	—
Rhamnus cathartica	0.06	0.83	0.14
Ribes cynosbati	—	0.01	0.15
Rubus spp.	15.57	13.31	4.23
Sambucus spp.	0.94	0.20	0.59
Sassafras albidum	4.70	3.78	0.51
Smilax hispida	0.28	0.04	1.44
Solanum dulcamara L.	—	0.20	—
Toxicodendron radicans	2.46	1.78	1.06
Vitis spp.	0.54	1.62	2.19
Total ± s.d.	32.1 ± 31.9	39.9 ± 36.5	20.7 ± 25.6
Student-Newman-Keuls	a	b	c
Tukey's HSD	a	a	b

Coverage by woody and herbaceous species in the ground-flora stratum was consistently approximately twice as high on burned treatment plots than on unburned plots in 1994 and 1995 (Tables 6–9). Differences in means for total coverage of herbaceous and woody ground flora species were significantly different for burned and unburned treatments (P = 0.0007) and blocking (P = 0.0001) in 1995 (Tables 8 and 9). Herbaceous ground-flora means for the biennial and once-burned treatments during 1994 and 1995 were not significantly different using Student-Newman-Keuls and Tukey's HSD ranked means tests (Tables 7 and 9). Differences between biennial and once-burned woody ground flora coverage means were not significant in 1994 (Table 6), but significant in 1995 using Student-Newman-Keuls tests, but not Tukey's HSD (Table 8). The Student-Newman-Kuels test has good power to detect differences between means, but does not control the maximum experiment-wise error rate (Einot and Gabriel 1975). Tukey's HSD controls the type I experiment-wise error rate, but has weaker power to detect type II errors (Hayter 1984).

The change in woody and herbaceous ground flora coverage of the three treatments during 1995 shows how rapidly the plots reburned in May of that year recovered (Fig. 1). Starting essentially at zero in May, reburned plots were 50% covered with new woody seedlings and sprouts in July (Fig. 1*a*), the same time at which maximum coverage occurred in the once-burned (59%) and unburned (36%) treatments. At season's end, the reburned plots had the highest cover of any treatment. Whereas maximum coverage (33%) of herbaceous vegetation did not occur in the reburned plots until September (Fig. 1*b*), it was higher than any other treatment from July onward. Buell and Cantlon (1953) also found that herbaceous cover increased with frequency of prescribed burning on sandy sites in New Jersey.

Relative frequency data for small woody seedlings show that burning had a small effect on species composition (Table 10). Only *Rosa* spp. was completely absent on burned plots, but its frequency on unburned plots was very low. Of the five taxa absent from plots burned biennially, only prickly gooseberry (*Ribes cynosbati*) and bush honeysuckle

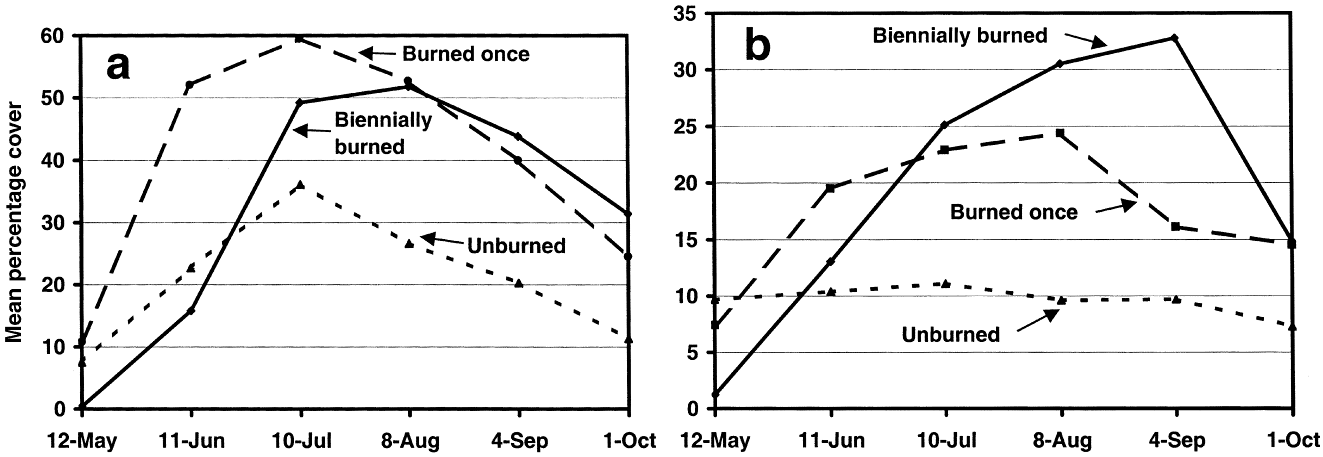

Fig. 1. Mean percentage cover by date during 1995 in biennially burned (1991, 1993, 1995), once-burned (1991), and unburned treatments. (*a*) Small (<1 m tall) woody seedlings and sprouts. (*b*) Herbaceous ground flora.

had frequencies on unburned plots >1.0. Among the major species, frequencies of *Acer* spp. and *Prunus* spp. declined, whereas *Quercus* spp., *Rubus* spp., and sassafras increased due to burning.

Table 9. Mean percentage cover of herbaceous ground flora in 1995 by burning treatment

Only species with ≥0.1 percentage cover are shown, but totals include all species. Totals with same letter are not significantly different (_= 0.05, d.f. = 300, *n* = 108)

Taxa	3 biennial burns	Burned once	Unburned
Apios americana	—	0.90	0.56
Apocynum androsaemifolium L.	0.96	—	—
Aralia nudicaulis L.	—	1.62	—
Arctium minus	—	0.15	—
Aster spp.	0.12	0.24	0.21
Circaea quadrisulcata	1.30	0.18	0.83
Desmodium glutinosum	0.65	0.03	—
Dryopteris spinulosa	2.04	7.58	3.00
Fragaria virginiana	—	0.34	—
Gallium spp.	0.45	0.54	0.72
Hieracium aurantiacum	—	0.47	—
Lactuca scariola	0.11	0.03	—
Maianthemum canadense Desf.	—	0.21	0.11
Moss	—	—	0.23
Osmarhiza claytoni	—	0.53	0.34
Phryma leptostachya	0.10	0.24	0.27
Phytolacca americana	7.81	1.84	—
Pilea pumila	4.95	0.04	0.23
Poa spp.	0.06	0.16	0.02
Polygonatum biflorum	0.06	0.99	0.38
Taraxacum officinale	0.12	0.12	0.02
Viola spp.	0.32	1.03	2.64
Total ± s.d.	19.3 ± 26.8	17.5 ± 24.1	9.6 ± 10.1
Student-Newman-Keuls	a	a	b
Tukey's HSD	a	a	b

Burning affected species composition of herbaceous ground flora quite differently than their woody counterparts; species diversity increased (Table 11). Only one minor species—*Floerkea proserpinacoides*—was completely absent in repeatedly burned plots, while once-burned plots contained every species present on unburned plots. On the other hand, 13 of the species found on burned plots were absent on unburned plots.

Table 10. Relative frequency of small (<1 m) woody seedlings in 1 m² subplots by burning treatment and year

Taxa	Biennial		Burned once		Unburned	
	1994 (2 burns)	1995 (3 burns)	1994	1995	1994	1995
Acer spp.	2.6	2.6	5.1	6.9	6.6	8.7
Berberis thunbergii	0	0	0	0.9	0	0.4
Carya spp.	0.9	0	0.7	1.0	0.19	0.4
Celastrus scandens	0	0.6	0	0	0	1.0
Diervilla lonicera	0	0	0.5	1.6	1.1	2.1
Fraxinus spp.	0.8	0	0.7	0.2	0.4	0.2
Parthenocissus quinquefolia	5.5	8.6	6.4	7.1	7.6	7.1
Pinus spp.	4.4	0.4	2.8	1.2	7.2	5.8
Prunus spp.	1.5	0	1.4	2.6	3.2	7.7
Quercus spp.	1.5	2.4	2.5	2.2	1.3	0
Rhamnus cathartica	2.7	0.6	3.3	2.3	3.4	1.4
Rhamnus frangula	0.3	0	0	0	0	0.5
Rhus spp.	1.1	0	0.4	0	0	0
Ribes cynosbati	0	0	0	0.2	0.8	1.7
Rosa spp.	0	0	0	0	0	0.2
Rubus spp.	8.2	14.4	10.0	11.4	7.0	6.3
Sambucus spp.	0.8	2.6	0.1	1.0	0.2	1.0
Sassafras albidum	5.3	6.6	5.5	5.5	4.6	3.1
Smilax hispida	0.8	0.4	0.4	0.3	1.0	0.4
Tilia americana	0	0	0.3	0	0.2	0
Toxicodendron radicans	2.8	4.9	1.7	2.8	4.0	5.2
Vitis spp.	1.7	3.2	3.8	3.1	1.7	2.1

Table 11. Relative frequencies of herbaceous ground flora in 1 m^2 subplots by burning treatment and year

Taxa	Biennial		Burned once		Unburned	
	1994 (2 burns)	1995 (3 burns)	1994	1995	1994	1995
Apios americana	13.7	2.6	11.8	4.7	2.7	1.9
Apocynum androsaemifolium	0.3	1.9	0.1	0	0	0
Aralia nudicaulis	0	0	0	0.6	0	0
Arctium minus	0.5	0	0.4	0.4	0	0
Aster spp.	0.9	1.5	3.0	2.6	1.0	1.6
Carex spp.	0.9	0	2.0	0	0.4	0.7
Circaea quadrisulcata	2.1	6.0	1.6	1.6	4.4	7.7
Cirsium spp.	0.2	0.6	0.4	0	0	0
Desmodium glutinosum	0.5	0.9	0.7	0.2	0	0
Dryopteris spinulosa	3.4	3.6	4.2	5.1	5.1	6.1
Floerkea proserpinacoides Will.	0	0	0.1	0	0.2	0
Fragaria virginiana	0.6	0	0.8	1.2	0.6	0
Gallium spp.	13.7	4.5	11.8	6.1	4.6	7.0
Geranium maculatum L.	0.3	0	0.3	0.3	17.1	0
Hieracium aurantiacum	0.5	0	1.0	2.2	0	0
Hypericum punctatum Lam.	0.2	0	0.3	0	0	0
Lactuca scariola	1.4	1.3	0.7	0.4	0	0
Maianthemum canadense	0.3	0	0.4	0.9	0.4	1.2
Mitchella repens	0	0	0.1	0	0	0
Moss	0.3	0	0.4	0	0.8	0.4
Osmorhiza claytoni	0.8	0	3.0	4.2	2.5	4.0
Oxalis acetosella	0	1.9	0.4	0.7	0	0
Phryma leptostachya	0.9	1.5	1.0	2.3	0	3.3
Phytolacca americana	4.0	8.8	1.3	2.3	0.4	0
Pilea pumila	2.1	7.28	0.3	0.4	0.4	0.7
Plantago major L.	0.2	0.2	0	0.7	0.2	0
Poa spp.	1.4	1.3	1.3	2.0	0.6	0.4
Podophyllum peltatum	0.2	0	0.4	0.2	0	0
Polygonatum biflorum	1.8	1.1	1.8	3.9	2.7	3.5
Potentilla simplex Michx.	0.2	0	0.3	0	0.2	0
Rumex acetosella	0	0.2	0.7	0.9	0	0
Taraxacum officinale	1.4	2.6	1.0	1.3	0.8	0.4
Trillium spp.	0.3	0	0	0	0	0
Verbascum thapsus L.	0.5	0.2	0.3	0.3	0	0
Viola spp.	5.3	4.7	2.5	3.6	4.6	5.9

Differences in ground flora species richness between unburned and once-burned plots were clear in both years (Table 12). Unburned treatments contained fewer species in 1994 and 1995 than once-burned plots. Plots burned biennially had greater species richness than unburned plots in 1994, but four fewer species in 1995. Following spring reburning in 1995, plots burned biennially had 11 fewer herbaceous species than they did in 1994, even though percentage cover was higher.

Ground flora communities exhibit distinct differences in density and species richness following repeated burning. Henning and Dickmann (1996) found that herbaceous cover on biennially burned treatments in a northern Michigan red pine stand was lower than on treatments with 5- and 10-year intervals between fire. However, species richness did not differ among burn treatments and between burned and unburned plots. By contrast, White (1983) noted that repeated prescribed fires increased overall species richness in a *Quercus ellipsoidalis* E.J. Hill community in Minnesota, a result similar to our own, except immediately after our reburn. Lemon (1949) showed that ashes on burned sites stimulate a lush early herb and shrub growth, although survival and increase of herbs are related to life history and form. In addition, the complete removal of the sapling and large woody seedling strata by burning undoubtedly altered the microclimate near the ground (though we did not measure it), stimulating ground flora growth.

Richness of woody ground-flora species differed little among treatments and years in our study (Table 12). Woody species on plots reburned in 1995 suffered top kill, but the

Table 12. Total number of ground flora (<1 m) species by year and burning treatment

Vegetation type	1994 2 biennial burns	1994 Burned once	1994 Unburned	1995 3 biennial burns	1995 Burned once	1995 Unburned
Herbaceous	30	32	22	19	26	19
Small woody seedlings	18	17	18	12	18	16
Totals	48	49	40	31	44	35

majority of species re-sprouted or germinated from buried seed. The lower overall species richness observed in 1995 was probably due to the difference in plot locations during successive years. The woody ground flora of unburned plots contained greater representation of species easily killed by fire or with higher shade tolerance than found on burned plots (Tables 6 and 8). Control plots had the greatest average percentage coverage and frequency of small seedlings of *Acer* spp., *Pinus* spp., *Prunus* spp., vine bittersweet (*Celastrus scandens*), and greenbriar (*Smilax hispida*).

Plots burned biennially were characterized by small woody seedlings and sprouts of fast-growing, disturbance favored species. Although most small woody stems were killed during the 1995 spring reburning, these plots were quickly vegetated by a dense regrowth, primarily of *Rubus* spp., sassafras and, to a lesser extent, poison ivy (*Toxicodendron radicans*) and Virginia creeper (*Parthenocissus quinquefolia*). By mid-summer, the *Rubus* and sassafras on the freshly burned plots had grown to about 1 m in height in most areas. Once-burned treatments also contained the greatest average coverage by small woody seedlings of the same species that characterized plots burned biennially—*Rubus* spp., sassafras, and Virginia creeper. In addition, oak seedlings were most common on the once-burned plots.

Sassafras appears to be the most important fire-favored hardwood tree species on this site. Prior to reburning in May of 1995, density of sassafras was very high on plots burned biennially. Although few stems survived the 1995 spring reburn, root suckers of sassafras quickly resprouted and were nearly ubiquitous after 2 months, although they didn't grow tall enough to be included in the large-seedling class. The once-burned plots also contained nearly four times the density of sassafras than unburned plots. Among the shrubs, species of *Rubus* clearly were the most important fire followers in our study, as they have been in others (Abrahamson 1984; Reich *et al.* 1990; Henning and Dickmann 1996). These two sprouting species should continue to be dominant components of the understory of this stand, particularly with repeated burning.

Burned treatments had greater overall coverage by most herbaceous species than unburned plots, although differences were not statistically tested at the species level. Unburned plots were dominated by spinulose shield fern (*Dryopteris spinulosa*) and violets (*Viola* spp.). The only herb taxon that diminished greatly immediately following fire (1995) was *Viola*, but the 1994 cover data and their relatively high frequency on the 1995 reburn plots indicate that they recovered quickly. Herbaceous flora in burned treatments reflect both the frequency of disturbance and the decreased shading by understory woody plants. In 1995 (season immediately after spring reburning), plots burned biennially were dominated by pokeweed (*Phytolacca americana*), nettle (*Pilea pumila*) and, to a lesser extent, enchanter's nightshade (*Circaea quadrisulcata*) and spinulose shield fern. Species coverage on these plots in the second season after prescribed burning (1994) appeared more like that of the once-burned plots, with greatest coverage again by pokeweed, nightshade, shield fern, and, additionally, violets and groundnut (*Apios americana*). Taxa with greatest coverage on once-burned plots in both years again included groundnut, pokeweed, shield fern, and violets.

Responses of two of the herbaceous taxa were especially noteworthy. Spinulose shield fern was present at high coverage and frequency in unburned as well as burned treatments and represents a species of wide habitat adaptability. Even in the year immediately following a spring fire (1995), it was fairly ubiquitous, and given its dominance in the single-burn plots, it will continue to increase in importance. Destruction of the fronds of this evergreen fern by fire apparently does not kill most plants because buried rhizomes are protected from heat injury and resprouting occurs before most competing vegetation becomes reestablished (Billington 1952). Fern spores also germinate readily on fire-sterilized soil (Oinonen 1967). In terms of habitat preference, pokeweed directly contrasts with shield fern. It was barely present in unburned plots but increased markedly as burning frequency increased, becoming by far the most common herb observed after repeated burning. This perennial apparently finds the blackened seed bed, lack of competition, and open understory environment following fire especially suitable for seed germination and establishment.

Conclusions

Introduction of fire into this mixed pine ecosystem produced significant changes in vegetative cover. As a major ecosystem process, fire shifted understory structure from a multistratum community dominated by small trees and shrubs to a monolayer of low woody sprouts and herbs. Visually the change is striking; during full leaf-out in summer unburned parts of the stand appear to be an impenetrable thicket, whereas burned areas are open, accessible, and visually appealing. Similar responses to fire have been noted in western (Fule and Covington 1994; Arno *et al.* 1995), southern (Brockway and Lewis 1997; Waldrop *et al.* 1987), and eastern (Little and Moore 1949; Buell and Cantlon 1953) pine ecosystems in North America.

As is common following many natural and anthropogenic disturbances (Reice 1994; Averill *et al.* 1997), post-fire species diversity in our study was either unchanged (woody plants) or increased (herbs). Among woody plants, species lost following prescribed burning included *Carpinus caroliniana*, *Celtis occidentalis*, *Cornus florida*, and *Zanthoxylum americanum*, but other species—*Viburnum* spp., *Liriodendron tulipifera*, and *Rhus* spp.—took their place. We noted no net losses in herb species, excepting the temporary drop that occurred immediately following a fire. Burning created a new niche in which fire-following species readily became established (Trabaud 1987), either from imported propagules or those lying dormant in the soil for many years awaiting the establishment stimulus provided by fire (Oinonen 1967; Ahlgren 1979; Abrams and Dickmann 1984).

The biennial burn cycle used as the extreme treatment in our experiment is more frequent than the pre-European settlement fire regime of red and white pine ecosystems in the Great Lakes Region (Maissurow 1941; Van Wagner 1970; Rouse 1988; Guyette *et al.* 1995). Nonetheless, the tolerance and resilience of the plant community to this extreme disturbance regime is remarkable. We also found that carabid ground beetles, a commonly studied index of species diversity, preferred the highly disturbed habitat provided by the biennial burning regime (Neumann 1997). Restoration of fire to pine communities may have many objectives (Dickmann 1993; McRae *et al*. 1994) but clearly plant diversity, especially among herbs, is enhanced. In some cases rare and endangered species are favored by fire, either directly or indirectly (Abrams and Dickmann 1984; Swengel 1994; Greenlee 1997), increasing the ecological benefits of fire. Based on our results and those of previous studies, an operational fire-return interval of 5–10 years in red and white pine stands managed to maximize ecological and other benefits would appear optimum. Restoration of such a fire regime, combined with a long timber rotation for the pine overstory, or no consideration for timber at all, could produce old-growth ecosystems reminiscent of those existing prior to European settlement.

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